

Structure and Organization of the Rhizome Vascular System of Four *Polypodium* Species

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ABSTRACT.—The present investigation is a detailed study of the vasculature of the rhizome of four species of *Polypodium* (*P. cambricum*, *P. fauriei*, *P. interjectum*, and *P. sibiricum*). The vascular architecture of the rhizomes of the *Polypodium* species studied denotes a line of reduction and simplification of characters. The characteristic nature of the association of branches with leaves in the species of *Polypodium* studied seems to be significant. Vascular morphology of the rhizome of *Polypodium* does not support a close relationship with *Goniophlebium* as has previously been hypothesized. However, more extensive study of *Polypodium* is needed to arrive at any definite conclusion.

KEY WORDS.—Polypodiaceae, rhizome, vascular system, *Polypodium*

The genus *Polypodium* is typified by *P. vulgare* Linn., a fern of the north temperate zone of the world. *Goniophlebium* is regarded by some taxonomists as congeneric with *Polypodium* while many prefer to regard it as separate genus (Rodl-Linder, 1990; Schneider *et al.*, 2004; Srivastava and Khare, 2005). Though predominantly a neotropical genus, *Polypodium* includes a few species in Africa and eastern Asia and one, *P. vulgare* Linn., the type species, in Europe.

Christensen (1938) redefined the genus *Polypodium*, excluding hundreds of species treated in it by earlier authors. At the same time he included *Goniophlebium* in the genus *Polypodium*, which he considered a natural genus of about 50 species in tropical and subtropical America, Europe and Asia to Polynesia. Ching (1940) merged *Goniophlebium* into *Polypodium* which he placed in tribe Polypodieae of the subfamily Polypodioideae. Holttum (1949), who recognized five groups within the Polypodiaceae, included *Goniophlebium* in *Polypodium*, which he placed in Phymatodes group. Copeland (1947) and de la Sota (1973) preferred to separate the palaeotropic species to constitute the genus *Goniophlebium*, which they regarded as closely related to *Polypodium s.s.* Nayar (1970, 1974) and Crabbe *et al.* (1975) included *Polypodium* and *Goniophlebium* in their subfamily Polypodioideae of the family Polypodiaceae. Pichi-Sermolli (1977) recognized 14 groups within the Polypodiaceae, one of them included the genera

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Polypodium and *Goniophlebium*. Tryon and Tryon (1982) and Rodl-Linder (1990) considered *Goniophlebium* an Old World genus with articulate pinnae and not closely related to *Polypodium* s.s., which is predominantly a New World genus. Hennipman *et al.* (1990) provisionally included *Goniophlebium* in *Polypodium* sensu lato, tribe Polypodieae of the subfamily Polypodioideae. Recently, Smith *et al.* (2006) included both in Polypodiaceae of the order Polypdiales under Polypodiopsida.

In the genus *Polypodium*, rhizomes are short to long creeping, the rhizome scales are peltate or pseudopeltate rarely basifixed and clathrate or opaque with a broad central band. Fronds are uniform, monomorphic and simple with the lamina usually pinnatifid or pinnate and with no laminar hairs or scales. Vascular morphology of the rhizome of ferns is currently well accepted as a conserved feature, which is minimally affected by the environment and is a highly reliable comparative criterion thought to be of significance in taxonomic and phyletic studies of homosporous ferns. Hence, the structure and organization of the vascular system in the fern shoot have been useful in comparative studies (Tansley, 1907–08; Bower, 1910, 1914, 1915, 1917, and 1918; Hayata, 1927, 1928; Tardieu-Blot, 1932; Ogura, 1972; Ching, 1940; Holttum, 1964; Nayar and Chandra, 1967; Nayar *et al.*, 1968). In recent years, pteridologists have also demonstrated the importance of the vasculature of the rhizome in phylogeny (Kato, 1972; Lucansky and White, 1974; Chandra and Nayar, 1975; Chandra and Kaur, 1976; Chandra, 1982; Chandra *et al.*, 2003; Hovenkamp, 1990; and Srivastava *et al.*, 2007).

Even with a long history of vasculature research, our knowledge of the vascular system of the rhizome of the genus *Polypodium* is meager, and, to date the only detailed description of the vasculature of the rhizome of *Polypodium vulgare* was provided by Srivastava and Khare (2005). The structure and organization of vascular system in the rhizome of most species of *Polypodium* remain almost unknown, except for few anatomical observations on the rhizome of *P. microrhizoma* Clarke ex Baker and petiole of *P. amoenum* Mett. (Bir and Trikha, 1980), and gross morphological details of *Polypodium formosanum* Baker and *P. glaucophyllum* Kunze (Hovenkamp, 1990).

The present investigation is a detailed study of the vasculature of the rhizome of four species of *Polypodium* (*P. cambricum* L., *P. fauriei* Christ, *P. interjectum* Shivas and *P. sibiricum* Sipliy) with more emphasis on the arrangement of leaf gaps, number and departure of the leaf trace strands, association between leaf gap/branch gap/leaf trace/branch trace, and association of mechanical tissue. Our goal is to assess the potential value of these characteristics in taxonomic and phyletic considerations.

MATERIALS AND METHODS

For the present study, four species of *Polypodium* were obtained from Russia through the courtesy of Dr. Nina M. Derzhavina, Herbarium, Orel State University, Russia. They are *P. cambricum* L. (N.M.Derzhavina 87, OHHI), *P.*

fauriei Christ (*N.M.Derzhavina* 10, OHHI), *P. interjectum* Shivas (*N.M.Derzhavina* 94, OHHI) and *P. sibricum* Sipl. (*N.M.Derzhavina* 15, OHHI).

Vasculature morphology was studied mainly from serial sections from hand as well as microtome sections (cut at 100–130 μm) of adult rhizomes fixed in F.A.A. and stored in 70% ethyl alcohol. Anatomical observations recorded here are based on microtome sections stained with safranin and fast green. Stelar organization was studied from three-dimensional reconstructions based on camera lucida tracings of the outline of the vascular strands in serial sections. Because of the significance of vascular organization in the rhizome of ferns in taxonomic and phyletic considerations, particular attention was paid to the general form and shape of the vascular cylinder, leaf gap, leaf trace, branch gap, branch trace and the association of the branch with the leaf.

RESULTS

Rhizomes are moderately stout (*P. cambricum* and *P. interjectum*) to soft and slender (*P. fauriei*, and *P. sibricum*) bearing leaves restricted to two alternating, dorsal rows. The diameters of the rhizome ranges from ca. 2 mm to ca. 8 mm. Branches are usually associated with leaves on the abaxial side away from the dorsal median plane of the rhizome.

Transverse section of the rhizome in any plane usually shows 9–12 cylindrical to sub-cylindrical vascular bundles, which are distributed roughly in a circle in the ground tissue. The rhizome is soft, parenchymatous with the ground tissue uniform (not differentiated into cortex and pith) and having dense starch deposits. Sclerenchyma strands, as found in other polypodiaceous ferns, are absent in the species of *Polypodium* studied here. The epidermis is single layered and consists of regularly arranged small, thin-walled, rectangular cells.

Form of the Vascular Cylinder

The vascular cylinder of the rhizome is basically similar to the common types in the Polypodiaceae and is a highly perforated dictyostele with much elongated lacunae forming a conspicuous loose reticulum (Figs. 1–4). It is pierced with two alternating, large overlapping leaf gaps on the dorsal side and many large lacunae elsewhere so that the vascular strands are slender and cylindrical. In all four species the vascular cylinder is dorsiventral with leaf gaps closely placed at the dorsal surface so that the successive ones of the two rows overlap conspicuously. The area of the vascular cylinder between the two rows of the leaf gaps is slightly thicker than others constituting a distinct dorsal median vascular strand.

Root traces are restricted to the ventral half of the vascular cylinder and originate as superficial, solitary vascular strands from the outer surface of the stelar cylinder. As the root traces passes through the cortex of the rhizome it acquires a thick sheath of sclerenchyma.

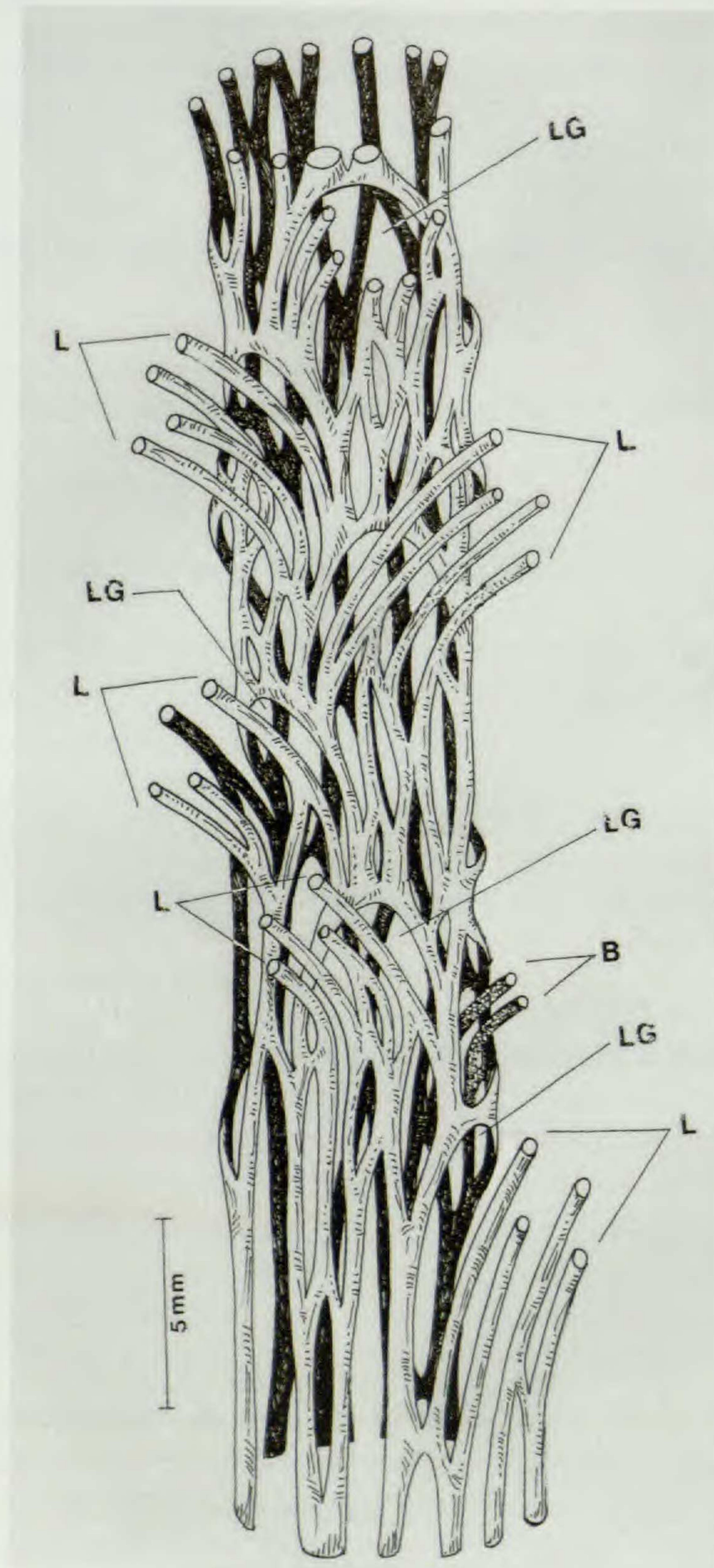
LEAF GAP.—Leaf gaps are usually oblanceolate in *P. fauriei* (Fig. 3, LG) and *P. interjectum* (Fig. 4, LG) with bluntly rounded anterior ends, while in *P. cambricum* (Fig. 1–2, LG) they are broad and ovate to oblanceolate with broadly rounded to bluntly rounded anterior ends. Leaf gaps of successive leaves overlap conspicuously and successive leaf gaps of the same side also overlap, though only slightly in *P. fauriei* and *P. interjectum*. In these two species the posterior end of each leaf gap extends downwards a little on either side of the anterior end of the next leaf gap so that the region between the two leaf gaps appears as a narrow, arched vascular strand.

In *Polypodium cambricum* and *P. sibiricum* the leaf gaps extend only a short distance beyond the region where leaf trace separates (i.e., the leaf trace strands are given off from the margins close to the anterior end of the leaf gap), while in *P. fauriei* and *P. interjectum* the leaf gaps are longer, extending markedly beyond the region of separation of the leaf trace (i.e., the leaf trace strands are given off from towards posterior margin of the leaf gap) as also reported in *P. vulgare* (Srivastava and Khare, 2005). However, in *P. interjectum* some of the leaf gap extends only a short distance beyond the region where the leaf trace separates.

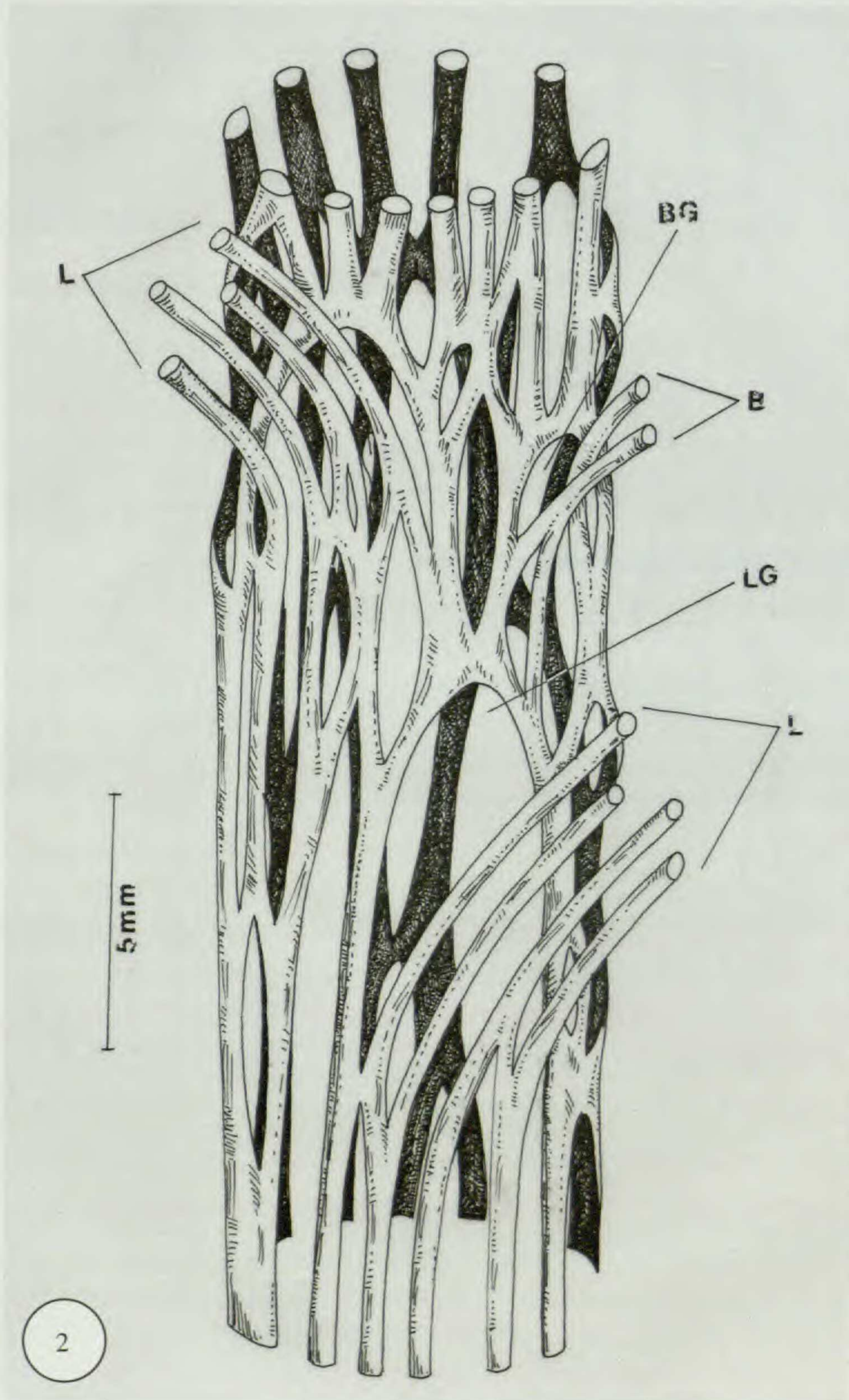
LEAF TRACE.—The leaf trace is highly dissected by profuse, short to elongated lacunae which are regularly placed towards the basal end of the leaf trace so that the basal region of the leaf trace often forms a closed-meshed reticulum. Each leaf trace is often composed of 4–8 slender vascular strands in the species of *Polypodium* studied. The leaf trace strands usually branch off from the margins close to the anterior ends of the leaf gaps in *P. cambricum* (Figs. 1–2, L) and *P. sibiricum* while in *P. fauriei*, and *P. interjectum* leaf trace strands usually branch off from the posterior margins of the leaf gaps (Fig. 3–4, L) making the vascular strands of the leaf trace appear as independent strands traversing the cortex of the rhizome. As in other Polypodiaceae described, the adaxial margins of the leaf trace are slightly thickened (so that the last pair of leaf trace strands is thicker than the others).

BRANCH GAP.—Each branch trace has a conspicuous branch gap, placed next to the ventral posterior end of the leaf gap of the associated leaf (*P. cambricum* and *P. fauriei*) and conspicuously overlapping with the associated leaf gap though distinctly separated from it by a slender vascular strand (Figs. 1–3, BG). In *P. interjectum* (Fig. 4, BG) and *P. sibiricum* the branch gaps are short, and intimately associated with the base of the leaf trace so that it appears to be a part of the reticulated base of the leaf trace (i.e., the branch gap is merged with the leaf gap becoming inconspicuous). However, in *P. sibiricum* the branch trace is often solitary, becoming inconspicuous and appears to originate from the leaf trace strands themselves. Successive branch gaps on the same side do not overlap.

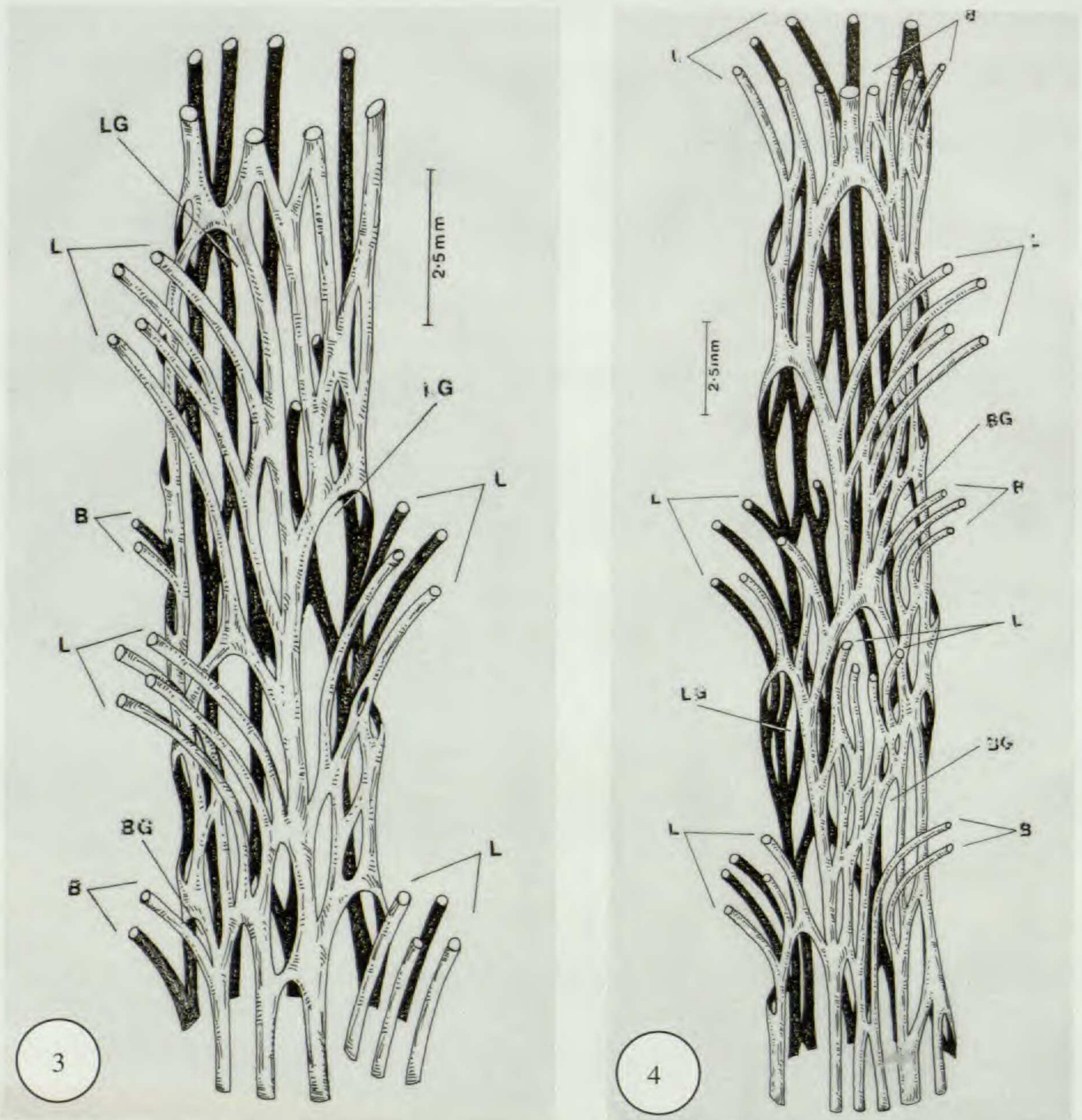
BRANCH TRACE.—As is characteristic of all Polypodiaceae, a branch is associated with a leaf at its abaxial side. Each branch trace is a simple structure, often composed of 2–4 slender, cylindrical vascular strands which do not form a



FIGS. 1-2. Vascular cylinder of a portion of the adult rhizome as seen from the dorsal surface. 1. *Polypodium cambricum*; 2. *P. cambricum* (B, branch trace; BG, branch gap; L, leaf trace; LG, leaf gap).



FIGS. 1-2. Continued.



FIGS. 3–4. Vascular cylinder of a portion of the adult rhizome as seen from the dorsal surface, **3**. *Polypodium fauriei*; **4**. *P. interjectum* (B, branch trace; BG, branch gap; L, leaf trace; LG, leaf gap).

reticulate vascular cylinder (Figs. 1–4, B). There is further reduction of the branch trace strands in *P. sibiricum* where the branch trace is often solitary. Also, in some of the leaves there is no branch associated with the leaves (Figs. 1, 3, and 4).

Structure of the Vascular Cylinder

The vascular cylinder of the rhizome is composed of usually 9–12 slender and mostly cylindrical vascular strands. Xylem tissue of each vascular strand is ribbon-like and tracheidal, 1–5 cells thick in *P. cambricum* (Fig. 5), 2–5 cells thick in *P. fauriei* (Fig. 6), 1–5 cells thick in *P. interjectum* (Fig. 7), 1–3 cells

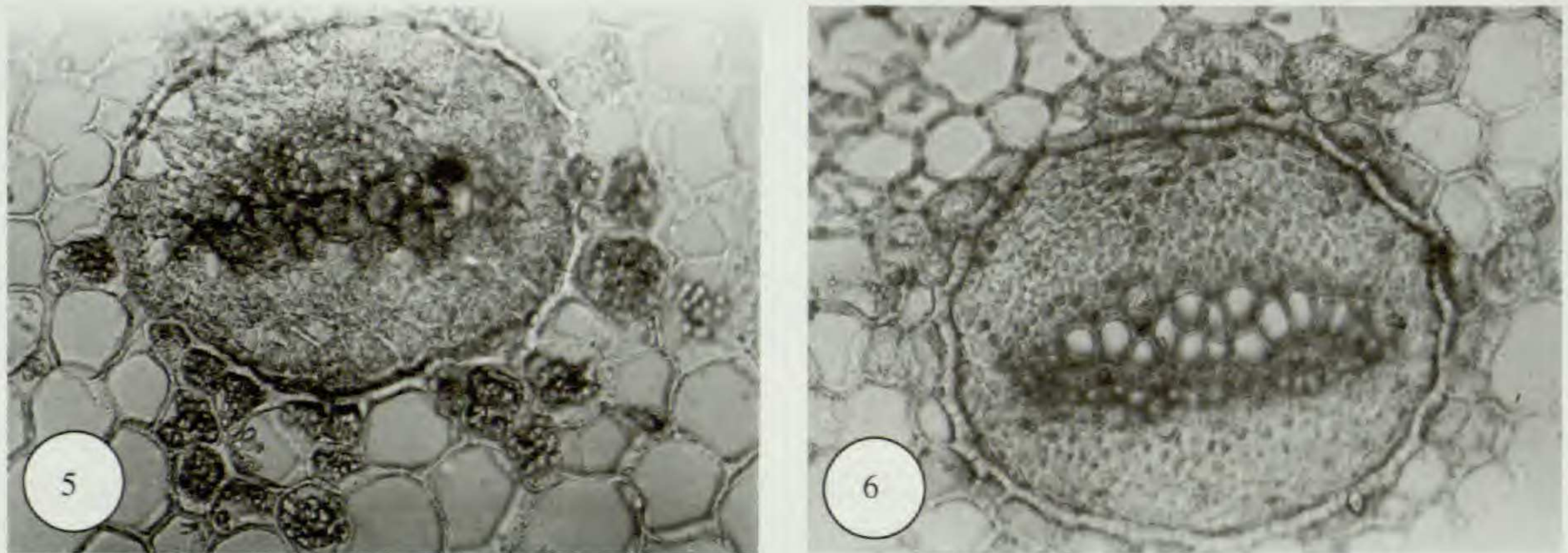
thick in *P. sibricum* (Fig. 8). The tracheids are interspersed with thin-walled individual cells or bands of xylem parenchyma in between in *P. cambricum*, *P. fauriei* and *P. interjectum* (Figs. 5–7) while in *P. sibricum* (Fig. 8), as in *P. vulgare* (Srivastava and Khare, 2005), the tracheids are not intermixed with xylem parenchyma. A thin sheath of 1–2 irregular layers of small parenchyma cells envelops the xylem tissue except at the free ends. The protoxylem is generally exarch in position, being present at the ends of the xylem tissue. The phloem is not continuous and is interrupted at the ends of the xylem tissue. Phloem is restricted to either surface of the xylem tissue and is interrupted at either end. It is massive, composed of 1–8 layers (*P. cambricum* and *P. fauriei*, 2–8 layers; *P. interjectum*, 2–4 layers; *P. sibricum*, 1–3 layers) of narrow, small, thin-walled parenchyma cells intermingled with few sieve cells. The pericycle is prominent, continuous around the vascular tissue, and consists usually of 1–2 layers of thin-walled, small regularly arranged polygonal parenchymatous cells. However, in *P. cambricum* and *P. fauriei* the pericycle is single layered consisting of broad, polygonal cells. The endodermis is well developed and composed of a single layer of rectangular, small, thin-walled cells with casparian thickenings on their radial walls. However, in *P. cambricum* the inner walls of the cortical parenchymatous cells abutting on the endodermis are usually thickened. Some of the endodermal cells have dark brown phlobaphene contents in their cells but there is no continuation in all the cells. The endodermis of some of the vascular strands are devoid of phlobaphene contents.

DISCUSSION

Polypodium is a fern genus of the north temperate regions of the world with a few species in Africa and eastern Asia. Holttum (1947) regards the Polypodiaceae as derived by reduction from *Phymatodes*, while *Polypodium* is regarded as an ancestral genus evolved independently of Microsorieae and Pleopeltideae by Copeland (1947). Copeland (1947) kept *Polypodium* as separate genus, most numerous in American tropics.

In general, open venation (simple, free) represents an ancestral condition but in ferns, especially Polypodiaceae, the most ancestral members have a complex netted venation, the few species with free veins being derived. Thus, according to Holttum (1947, 1964) reversion has taken place in Polypodiaceae. Mickel (1982) also considers the veins in the more recently derived groups free.

The restricted distribution of free venation, found only in the *Polypodium*-group, suggests strongly that reticulate venation is an ancestral character in the Polypodiaceae. The north-temperate *Polypodium* does not represent the ancestral condition, but the late offshoot of a tropical stock. *Polypodium* species have free veins but are connected by intermediates with the species which have anastomizing veins (more ancestral members in *Polypodium* have anastomizing veins).



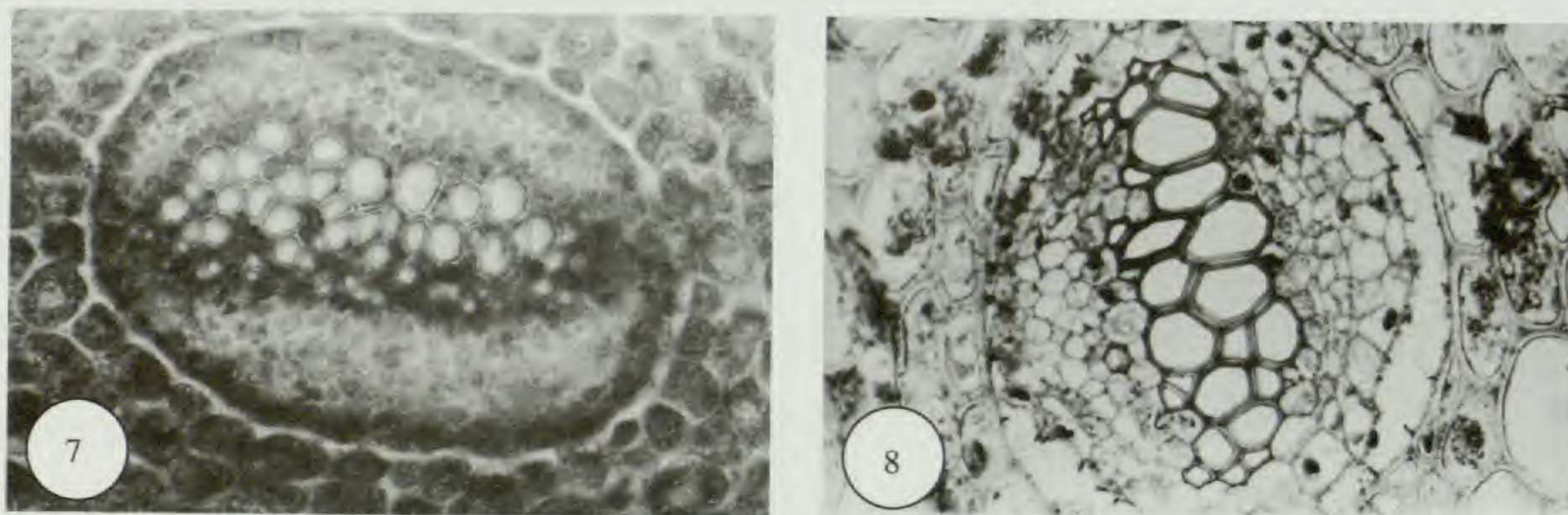
FIGS. 5–8. Transsections of the adult rhizome showing cellular organization of a vascular strand. 5. *Polypodium cambricum*; 6. *P. fauriei*; 7. *P. interjectum*; 8. *P. sibricum* ($\times 400$).

In contrast to *P. vulgare* (Srivastava and Khare, 2005) the dorsal median vascular strand is distinct and slightly thicker than other vascular strands of the rhizome in all the four species studied here. Recently, Smith *et al.* (2006) stated that the xylem is usually mesarch in the shoot of Monilophytes (including Eu- and Leptosporangiate ferns). However, contrary to the above observations, the protoxylem is restricted to either narrowed margins (lobes) of the xylem band on the side facing the cortex of the rhizome i.e., protoxylem is exarch in all of the species studied.

Each leaf trace in the *Polypodium* species is highly dissected and usually composed of 4–5 slender vascular strands while in *P. sibricum* it consists of 5–8 vascular strands. In contrast to *P. vulgare* (Srivastava and Khare, 2005) the leaf trace strands usually branch off from the margins close to the anterior end of the leaf gaps in *P. cambricum* and *P. sibricum* while in *P. fauriei* and *P. interjectum* the leaf trace strands branch off from the posterior margin of the leaf gaps. However, in *P. interjectum* some of the leaf gap extends only a short way beyond the region where the leaf trace separates. In *P. cambricum* and *P. sibricum*, the leaf gaps extend markedly on the posterior end of the leaf trace as found in the comparatively primitive species. In other species such as *P. vulgare* (Srivastava and Khare, 2005) and *P. interjectum* the leaf gap extends only slightly on the posterior side of the leaf trace.

Branch gaps are comparatively very short and often merged with the leaf gaps becoming inconspicuous (*P. interjectum*). There is further progressive reduction of the branch trace strands in *P. sibricum*. The branch trace is often solitary without any branch gap and is often merged, becomes inconspicuous, and appears to originate from the leaf trace strands themselves; thus forming an integral part of the leaf trace.

Perhaps the most interesting morphological feature of the rhizome is seen in *P. interjectum* and *P. sibricum* where the characteristic association of branch trace/gap with the leaf trace/gap is observed. In some cases the branch trace/gap is often merged with the leaf trace/gap, becoming inconspicuous and forming an integral part of the leaf trace/gap. Such type of association has also



FIGS. 5–8. Continued.

been reported in *P. vulgare* (Srivastava and Khare, 2005) and *Pleopeltis tweediana* (Hook.) A. R. Smith (Srivastava and Chandra, unpublished data). The absence of associated branches with some leaves and the closer associations of leaves and branches in *P. interjectum* and *P. sibiricum* seem to be significant and may indicate the evolutionary status of the taxa. Possibly the condition where the branch gap/trace extends to the leaf gap/trace is relatively more advanced than where the branch gap/trace is distinct and lateral to the leaf gap. Based on this it has been suggested that the vascular architecture of the rhizome in *Polypodium* species studied possibly exhibits a derived condition. However, the evolutionary significance of this association between leaf and branch needs more extensive investigation.

Relationship to Goniophlebium.—*Goniophlebium* was regarded by some taxonomists as congeneric with *Polypodium* (Christensen, 1938; Holttum, 1949; Hennipman *et al.*, 1990). However, many prefer to treat it as separate genus (Ching, 1940; Copeland, 1947; Holttum, 1968; Pichi-Sermolli, 1977; and Srivastava and Khare, 2005) most numerous in American tropics and maintain it as comparatively ancestral and intimately related to *Polypodium*. However, Tryon and Tryon (1982), considered *Goniophlebium*, an Old World genus with articulate pinnae, as not closely related to *Polypodium s.s.*, which is predominantly a New World genus.

Based on molecular studies, Schneider *et al.* (2004) showed that *Goniophlebium* is more distantly related to *Polypodium* than has been suggested. They further indicated that *Goniophlebium* is part of a large Old World clade that includes various genera such as *Lecanopteris*, *Lepisorus*, and *Microsorium*. They also provided evidence for a monophyletic *Goniophlebium*, as defined by Rodl-Linder (1990).

The differences in the vasculature of the rhizome observed here do not support a close association of *Polypodium* with paleotropic *Goniophlebium*. The results are consistent with the studies from molecular analyses (Schneider *et al.*, 2004), which suggested that *Goniophlebium* is more distantly related to *Polypodium* than previously suggested. In contrast to *Goniophlebium* (Srivastava and Khare, 2005) *Polypodium* species possess 1) dorsal median vascular strands scarcely different from other vascular strands, 2) usually

obliquely placed leaf gaps, 3) Leaf trace usually with four vascular strands, 4) much reduced branch trace usually with 1–3 vascular strands, 5) narrow branch gap which is less than half as long as the leaf gap, 6) Branch trace/gap in some cases merge with the leaf trace/gap forming integral part of it, 7) in some cases no branch associated with leaves, and 8) no sclerenchyma strands in the ground tissue. Until details regarding a large number of *Polypodium* species become available, an evaluation of the significance of stelar architecture in this group will not be possible.

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